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Seed predation on the dipterocarp *Neobalanocarpus heimii* (Dipterocarpaceae) by the clearwing moth *Synanthedon nautica* (Lepidoptera, Sesiidae) in Peninsular Malaysia

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Abstract Although sesiids have been considered one of the major seed predators of dipterocarp trees in Southeast Asia, little has been documented regarding their mode of predation. We investigated the mode of seed predation by *Synanthedon nautica* (Meyrick, 1932) (Sesiidae) on *Neobalanocarpus heimii* (Dipterocarpaceae), a tree species that produces high-quality timber, at Pasoh Forest Reserve in Negeri Sembilan, Peninsular Malaysia. In total, ten individuals of *S. nautica* emerged from 283 seeds of various sizes. All *S. nautica* were found in mature seeds that had the ability to germinate (seeds≥3.0 g), suggesting that *S. nautica* feeds on mature seeds. The length of time for *S. nautica* to emerge from the seed varied from 13 to 42 days (31.3 days on average). Time to adult eclosion was not dependent on seed weight. The biological adaptation of *S. nautica* to mast fruiting of dipterocarps in Southeast Asia is discussed.

Key words Dipterocarpaceae, mast fruiting, *Neobalanocarpus heimii*, seed predation, *Synanthedon nautica*.

Introduction

Neobalanocarpus heimii (King) Ashton (Dipterocarpaceae), known locally as Chengal, is an endemic tree species of Peninsular Malaysia and south Thailand (Appanah & Turnbull, 1998). It is one of the dominant emergent tree species in lowland dipterocarp forest in these areas, and its heavy, hard wood provides the best-known timber in Peninsular Malaysia (Elouard & Blanc, 2003). However, demand for its timber has resulted in high logging pressure for this tree species, and it now grows only in restricted areas and is categorized as vulnerable in *the IUCN Red List of Threatened Species*. Information on the reproduction of *N. heimii* is therefore required for its appropriate management and conservation.

Seeds play an important role in plant reproduction. However, the causes of seed loss for *N. heimii* have not been studied sufficiently. Elouard and Blanc (2003) reported that seed loss before germination is mainly caused by predation by insects such as moths of the genera *Assara*, *Caterema* (both Pyralidae), and *Andrioplecta* (Tortricidae), and scolytid beetles of the genera *Coccotrypes* and *Poecilips* (both Coleoptera: Scolytidae). They noted that the main fruit feeder was a moth of the genus *Assara*.

Sesiids (Lepidoptera: Sessidae) are one of the major seed predators of dipterocarp trees in Southeast Asia (Chey, 2002; Nakagawa *et al.*, 2003; Robinson *et al.*, 1994, 2001; Toy, 1988). *Synanthedon nautica* (Meyrick, 1932) (Lepidoptera: Sesiidae) has also been recorded as a seed predator of *N. heimii* (Robinson *et al.*, 2001). This species is a small (alar ex-

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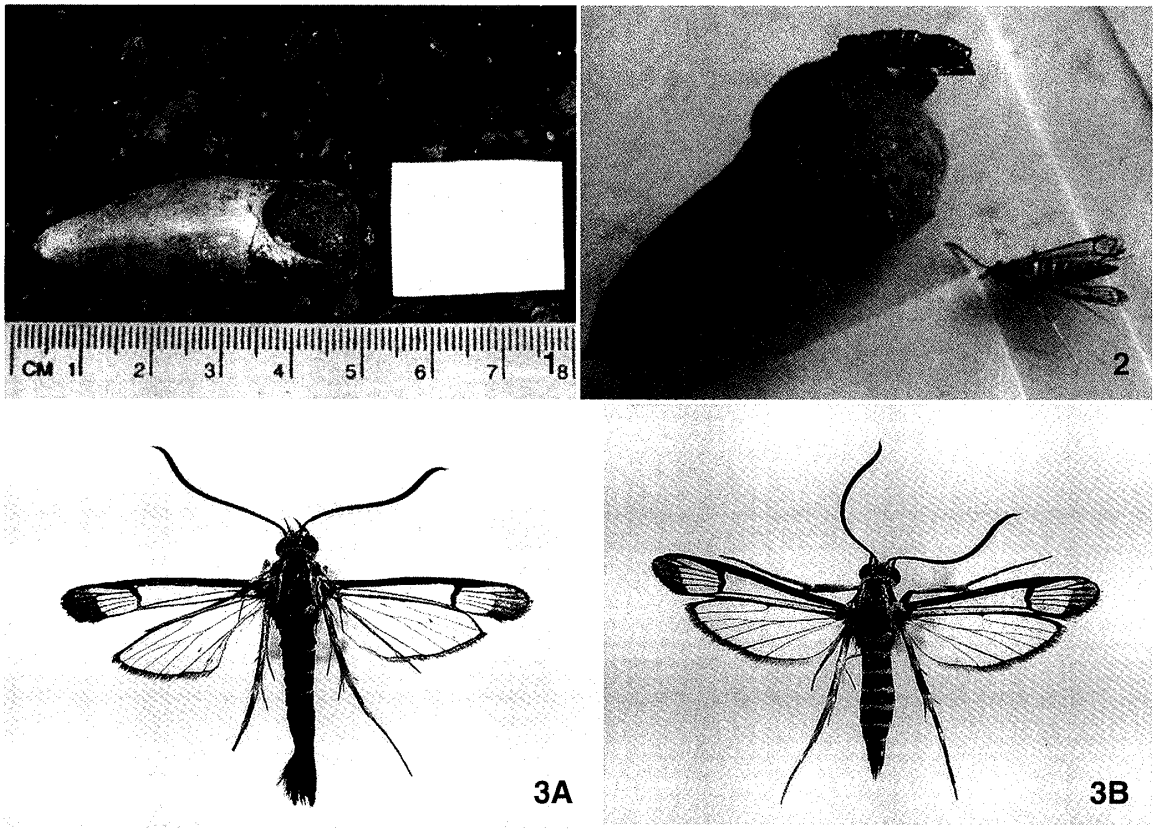

Figs 1–3. *Neobalanocarpus heimii* and *Synanthedon nautica*. 1. Mature fruit of *N. heimii*. 2. Pupal shell of *S. nautica* protruding from the calyx of an *N. heimii* fruit and an adult *S. nautica*. 3. Adults of *S. nautica*: (A) male, (B) female.

panse 17 mm), wasp-mimicking moth with transparent wings and a black-and-yellow striped abdomen (Figs 3A, B). Sesiids are distributed worldwide, and more than 150 species are known from Southeast Asia. Larvae of this family are often stem, bark, or root borers. The larvae of *S. nautica*, however, develop in the seed or fruits of *Dipterocarpus grandiflorus*, *Hopea heimii*, *Parashorea densiflora*, *Shorea* spp., and *N. heimii* (Robinson *et al.*, 2001). However, little has been documented regarding the mode of predation by sesiids, including *S. nautica*. Here, we report predation of *N. heimii* seeds by *S. nautica*, focusing on the relation of predation to seed size.

Materials & methods

Fruits of *N. heimii* were sampled in a 50-ha and a 40-ha permanent plot in Pasoh Forest Reserve (2°59′N, 102°18′E; 75–150 m a.s.l.), Peninsular Malaysia. Pasoh Forest Reserve is located approximately 70 km southeast of Kuala Lumpur, the capital of Malaysia, and is a lowland dipterocarp forest in which there are numerous young and mature *N. heimii* trees. In the 50-ha permanent plot, 158 stems≥10 cm in diameter were recorded for *N. heimii*, of which 60 reached 100 cm in diameter (Kochummen, 1997), making it the second most abundant dipterocarp species in the plot.

Fruits of *N. heimii* are hard, heavy (around 10 g when fully developed), green, and hold a single seed (Fig. 1). Unlike most other dipterocarp fruits, they lack wings. Therefore, they fall beneath the mother tree.

The fruiting behavior of *N. heimii* differs from that of most other dipterocarps in two respects. First, *N. heimii* bears flowers and fruits almost annually (Marzalina *et al.*, 2003). Dipterocarps in Southeast Asia are known for their unique mast fruiting phenology; they do not fruit every year, but superannually (2- to 10-year intervals) and synchronously among different species (Appanah, 1993). Thus, *N. heimii* flowers and fruits more frequently than other dipterocarps. Second, the fruit dispersal period of *N. heimii* is much longer than that of other dipterocarps. Seeds of *N. heimii* mature, *i. e.* become germinable, 6 months after flowering, and mature seeds continue to be dispersed for more than 1 year (Naito *et al.*, 2005). In contrast, seeds of most other dipterocarps disperse synchronously within 1–2 months of maturity. The unique fruiting behavior characteristics of *N. heimii* allow seeds to be collected at almost any time of the year.

Fruits sampling was carried out from August to October 2002, during a mast fruiting period in Pasoh (*cf.* Numata *et al.*, 2003), and in July 2003, outside of the mast fruiting period.

Green, newly fallen fruits of various sizes were collected from beneath the canopies of nine *N. heimii* mother trees. The fruits were maintained in a laboratory in Simpang Pertang, a town near Pasoh Forest Reserve, for observation of emerging insects.

Sampled fruits were sorted by size. Fruits of similar size were weighed together (≤5 fruits), and the mean weight of similar-sized fruits was used as an estimate of individual fruit weight. The fruits were placed in a plastic box (175 × 120 × 37 mm) lined with wet paper to rear the insects. Because *N. heimii* fruits are acorn-like, we hereafter refer to them as seeds and regard fruit weight as seed weight.

The rearing boxes were checked almost every day. The number of adult insects and time to emergence were recorded. The number of seeds that germinated (*i. e.* when the radicle extended from the pericarp) was also counted to determine the germination rate. Because mature seeds of *N. heimii* readily germinate in 1 week without dormancy when they fall, we expect the obtained germination rate to reflect the germination rate under natural conditions or in a nursery.

Results

In total, 283 seeds were collected, and 108 seeds germinated in the rearing boxes (Table 1). Seed weight ranged from 0.36 to 12.7 g.

Ten adult *S. nautica* emerged from the seeds, of which three emerged from seeds collected during the mast fruiting period and seven emerged from those collected outside of the mast fruiting period. Some weevils (Coleoptera: ?Nanophyinae), scolytids, and species of moths from other genera (*Assara*, *Lamoria*, *Andrioplecta*, and *Stathmopoda*) also emerged from the seeds. The mean time from seed collection to the emergence of adult *S. nautica* was about 1 month (mean±SE=31.3±0.8 days) and ranged from 13 to 42 days. This variation

Table 1. Number of *Neobalanocarpus heimii* seeds sampled, number of seeds that germinated, and number of *Synanthedon nautica* that emerged from immature (≤2.9 g in weight) and mature (≥3.0 g in weight) seeds.

Seed maturity	Sampled	Germinated	*S. nautica* emerged
Immature (≤2.9 g)	106	0	0
Mature (≥3.0 g)	177	108	10
Total	283	108	10

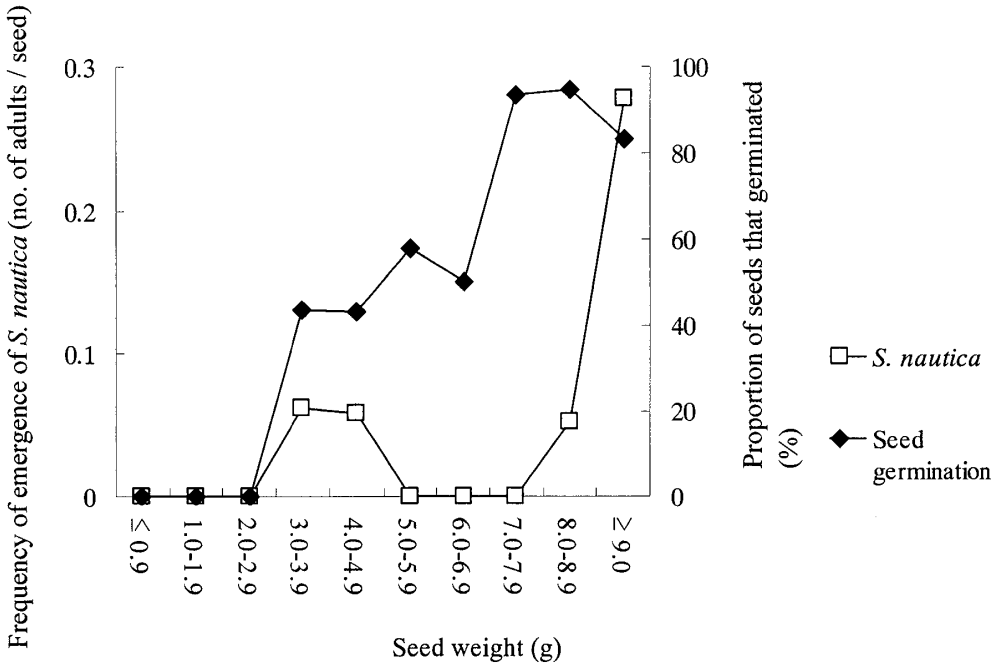

Fig. 4. Frequency of emergence of *Synanthedon nautica* adults from seeds of *Neobalanocarpus heimii* and the proportion of seeds that germinated for each seed weight class.

may have been due to differences in the timing of when seeds fell from the mother trees. Thus, insects that emerged from smaller seeds that had been dispersed earlier may have taken longer for emergence than those from larger seeds that had been dispersed later. However, the time to emergence seemed not dependent on seed weight (y=0.045x+31.7, where x: days for emergence, y: seed weight [g], r^2=0.0003, P=0.96).

The pupal shell could be seen protruding from the pericarp of the seed after adult eclosion (Fig. 2). Usually, one adult moth emerged from each infested seed. The larvae did not consume the whole cotyledon, but only part of the seed. Therefore, seeds that had been attacked could sometimes still germinate. However, none of the germinating seeds that had been attacked completed elongation of the radicle; each seed died before the radicle reached its full length. Therefore, predation by *S. nautica* had a serious negative effect on seed viability.

The seeds were divided into ten classes based on seed weight; each class was composed of ten or more seeds. The frequency of emergence of *S. nautica* from the seeds and the proportion of seeds that germinated are shown in Fig. 4. Only seeds that were in the 3.0–3.9 g or heavier weight classes germinated. Thus, we defined seeds that weighed at least 3.0 g as mature, and seeds that weighed less than 3.0 g as immature (*i. e.* seeds that dropped prematurely before they were sufficiently developed to germinate). Seeds were up to four times larger than 3.0 g, and the germination rate increased with seed size, reaching more than 80% when seed weight exceeded 7.0 g.

Synanthedon nautica emerged only from mature seeds. Although the number of seeds that were collected and the number of adult moths that emerged were small, the proportion of seeds from which *S. nautica* emerged was significantly higher in mature seeds than in immature seeds (Fisher's exact test, P=0.008; Table 1). The highest rate of emergence, 0.28 moths per seed, occurred in the heaviest seed weight class (≥9.0 g).

Discussion

Synanthedon nautica emerged only from mature seeds, *i. e.* seeds that weighed≥3.0 g at the time of collection. Naito *et al.* (2005), however, showed that more than 30% of seeds that weighed less than 2.5 g germinated in a nursery. This difference in the minimum weight of seeds that could germinate may reflect the fact that there was some variation in mature seed weight among mother trees or that the condition of our germination test was insufficient for the smaller mature seeds. In any case, *S. nautica* emerged only from larger, developed seeds, and two possible explanations could account for this. One is that *S. nautica* adults may lay eggs only on older seeds. In this case, no adult moths would emerge from immature seeds because they would have been aborted before eggs could have been laid on them in the canopy. The other possibility is that *S. nautica* adults do lay eggs on young seeds, but larvae in immature aborted seeds cannot develop sufficiently to survive to the adult stage. Dissection of immature seeds would be required to determine if this is the case and to shed further light on the timing of oviposition in *S. nautica*.

One of the most discussed questions about seed predators of dipterocarps is how they survive during long non-fruiting periods (Janzen, 1974; Toy, 1991). However, for the seed predator *S. nautica*, its host, *N. heimii*, fruits almost every year. Furthermore, *N. heimii* is abundant in Pasoh Forest Reserve and can retain its seeds for more than 1 year after flowering.

Although we examined additional seeds from 12 *Shorea* species (*S. acuminata*, *S. bracteolata*, *S. dasyphylla*, *S. hopeifolia*, *S. lepidota*, *S. leprosula*, *S. macroptera*, *S. multiflora*, *S. maxwelliana*, *S. ovalis*, *S. parvifolia*, and *S. pauciflora*) and three *Dipterocarpus* species (*D. crinitus*, *D. cornutus*, and *D. costulatus*) during the mast-fruiting period of 2001–2002, *S. nautica* was not found in seeds of any of these species. Thus, the population of *S. nautica* in Pasoh Forest Reserve, and possibly in the rest of Peninsular Malaysia, is probably maintained by the continuous availability of *N. heimii* seeds, which is a rare case among dipterocarp seed predators.

A question of interest is how *S. nautica* populations are sustained in regions where *N. heimii* does not occur, such as Borneo. The holotype of *S. nautica* in the Natural History Museum of London was collected from Borneo (Meyrick 1932). It remains to be discovered whether the species has alternative hosts that produce fruits almost annually like *N. heimii* in these regions or whether the adult moths have a prolonged lifespan that enables them to survive until the next mast-fruiting event. Further studies of the biology of *S. nautica* in such regions are required to resolve this question.

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摘　　要

半島マレーシアにおけるスカシバガ *Synanthedon nautica* による *Neobalanocarpus heimii* (フタバガキ科) の種子食害 (保坂哲朗・有田　豊・Laurence G. KIRTON)

スカシバガは東南アジアのフタバガキ科樹木にとって重要な種子食昆虫の1つと考えられているが, その食害の実態は殆ど報告されていない. 著者らは, 優良材で知られる *Neobalanocarpus heimii* (フタバガキ科) の種子に対する *Synanthedon nautica* (スカシバガ科) の食害の実態を, 半島マレーシアネグリセンビラン州のPasoh森林保護区において調査した. 落下後間もない様々な発育段階の種子計283個から, 10個体の *S. nautica* が得られた. *S. nautica* はいづれも発芽能力のある成熟種子 (種子重3.0 g以上) より得られ, *N. heimii* の成熟種子を加害する種であることが分かった. また, 種子を拾ってから *S. nautica* の成虫が羽化するまでは13–42日 (平均31.3日) とばらつきがあったが, これと種子の重さとの間に

は相関関係は見出されなかった. 東南アジアにおけるフタバガキ科の一斉結実現象に対する *S. nautica* の適応について考察した.

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